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THE SKULL AND MANDIBLE OF *CONOHYUS*, A PRIMITIVE SUID FROM THE SIWALIK BEDS OF INDIA

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INTRODUCTION

Conohyus, a genus proposed by Pilgrim in 1926,[1] is a suid of mid-Tertiary age, found in the Lower Siwalik beds of northern India. It is closely related to *Hyotherium*, the typical Miocene pig of Europe, from which genus it differs by certain aberrant specializations which will be described below.

Hitherto our knowledge of *Conohyus* and *Hyotherium* has been based on dentitions and fragmentary skulls, and consequently it has been rather incomplete. A skull and a mandible of *Conohyus*, of which a detailed account will be given in this paper, as well as various dentitions —all collected by Mr. Barnum Brown in the Northern Punjab of India during the field season of 1922—add greatly to our knowledge as to the cranial anatomy of the Miocene Suidae.

The illustrations in this paper were made by Margaret Matthew.

THE SKULL.—The skull and mandible here described have been identified as *Conohyus sindiense* (Lydekker).

The skull, Amer. Mus. 19616, which was collected at a point stratigraphically 1600 feet above the level of Chinji Rest House, Punjab, and linearly one and one-half miles north of that location, was badly crushed and broken when found. The several fragments constituting it have been assembled to the best of our ability, and all in all they go to make up a reasonably complete specimen. This skull is of medium size, representing an animal somewhat comparable to the Babirussa pig in its proportions. It is, generally speaking, long and slender, and as might be expected of a Miocene suid, is distinguished by the small size of its brain case.

When viewed from the side, the skull is seen to have an essentially straight cranial profile, with but a slight dip or "stop" just above the orbit, a character typically suilline in its expression. The muzzle would seem to be relatively slender, much as in *Palaeochoerus*,[2] with a slight preorbital depression immediately anterior to the orbit. The infraorbital foramen has its anterior opening above the anterior border of the

[1] Pilgrim, G. E. 1926. 'The Fossil Suidae of India.' Mem. Geol. Surv. Ind., Pal. Ind., N.S., Vol. 8, No. 4, p. 12.

[2] For comparisons with *Palaeochoerus*, reference is made to the figures by Filhol, M. H. 1880. 'Mammifères fossiles de Saint Gerand le Puy,' Bib. de l'École des Hautes Études, Sec. des Sci. Nat., Tome 20, Art. 1, plates 4–10.

Also see Pearson, H. S. 1927. 'On the Skulls of Some Early Tertiary Suidae, etc.,' Phil. Trans. Roy. Soc. Lond., Ser. B, Vol. 215, p. 392. (Comment on Filhol's figures.)

third premolar, a position similar to that in *Palaeochoerus*, and one especially typical of the more primitive Suidae. That *Conohyus* is a specialized form is especially well illustrated by the heavy development of the zygomatic arch. In *Palaeochoerus* the arch is of normal size, relatively comparable to the arch in a female *Sus*, originating above the third molar and being of fairly uniform height along the extent of its length, while in *Conohyus*, the zygomatic process of the maxilla has become greatly expanded, so that the lower border of the arch extends down below the occlusal line. In conjunction with this expansion of the arch is its strong connection with the ascending portion of the maxilla. The zygomatic process, instead of arising from an anteroposteriorly short pedicle, is joined to the side of the face by a lengthened junction, extending from above the mid-portion of the third molar to a point above the third premolar. This connection of the arch with the vertical portion of the maxilla takes the form of a ridge, merging above into the preorbital depression, and below into the lower border of the arch, and terminating abruptly in front as a knob-like protuberance. Since the arch is extended downwardly, there is a long narrow pocket or furrow beneath this connection with the maxilla, which must have furnished room for a strong buccinator muscle. The lower border of the zygomatic arch reaches its lowest extension opposite the pterygoids, and from thence rises rapidly to the level of the glenoid.

The orbit is relatively small, as in other pigs, and is but partially closed behind by the postorbital processes of the maxilla and of the frontal. There is a small lacrymal bursa in the usual place, on the front border of the orbit.

The brain case, being small, becomes very narrow opposite the post-glenoid border, and this has necessitated the development of large sagittal and lambdoidal crests for the attachments of the temporal muscles. Such a character is typical of many primitive mammals, and in *Conohyus* is a direct inheritance from *Palaeochoerus*. The supraoccipital and the adjacent bones extend far back and overhang the condyles. The glenoids are fairly well raised above the occlusal line, being placed about as in the modern *Sus*. It might be well to say, in passing, that this normal position of the glenoids is the factor causing the expanded zygomatic arch to extend below the occlusal line. In *Phacochoerus*, for instance, the arch is deeply expanded, but due to the height of the glenoid the lower border of the arch is raised to quite a distance above the occlusal line.

At this point we may consider briefly the question of preorbital and postorbital lengths. As was shown by Osborn[1] and Gregory, the primitive perissodactyls are characterized by the close equality between the length of the face in front of the anterior border of the orbit, and the length of the cranium behind that same point. From such primitive forms, various lines of evolution followed separate trends, in some of which, such as the horses, the face increased greatly in length, while in others, like the titanotheres, it became extremely short. Turning now to the Suidae, we see that the primitive members of the family are marked by the approximate equality of preorbital and postorbital lengths, while among the advanced forms the tendency is for the face to become in-

[1]Osborn, H. F. 1929. 'The Titanotheres of Ancient Wyoming, Dakota and Nebraska.' U. S. Geol. Surv., Monograph 55, Pt. 2, pp. 820–834. (With the coöperation of W. K. Gregory.)

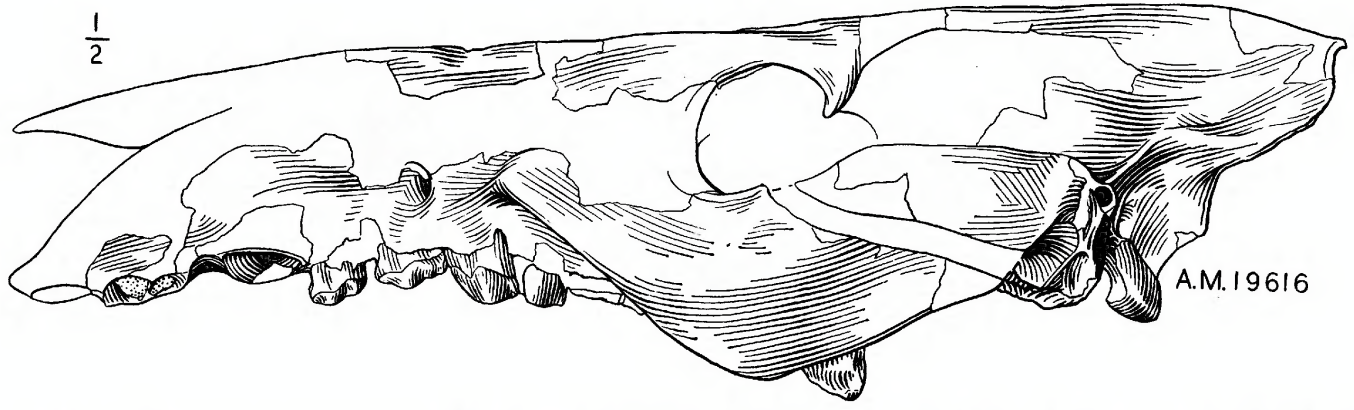

Fig. 1.—*Conohyus sindiense* (Lydekker). Amer. Mus. No. 19616. Side view of skull, one-half natural size. The specimen has been crushed, so that its true height would be somewhat greater than shown in the figure. (See Fig. 5 for restoration.) Restored portions unshaded.

creasingly long. Thus, in the skull of *Palaeochoerus* (as measured from Filhol's figure) the preorbital length is to the postorbital length as 110 is to 100, a fact that argues strongly in favor of the consideration that *Palaeochoerus* is close to the ancestor of all of the Suidae. *Conohyus* shows a slight advance in the increase of facial length as compared to cranial length, the ratio here being about 133 to 100. In the later suids the increase becomes greatly accentuated, reaching a ratio of 220 to 100 in the modern *Sus*. *Phacochoerus*, a relatively recent offshoot from the *Sus* line, is extremely specialized in that the face is four and a half times as long as the postorbital length.

These figures are inserted to show that *Conohyus* is but little advanced beyond the primitive *Palaeochoerus* type as to the ratio between facial and postorbital lengths. Thus it becomes apparent that most of the specializations of the suid skull which are closely associated with the lengthening of the face, have occurred in post-Miocene time.

The striking feature of the skull, as seen from the top, is the constricted brain case, which in *Conohyus* seems to show little if any advance in relative size over the brain case of *Palaeochoerus*. As a corollary to the unexpanded cranium, the zygomatic arches at their posterior limits stand out prominently from the skull, and from their posterior borders the occiput extends far back, being constricted at its proximal boundary, and flaring somewhat at the lambdoidal crest.

The palate is largely destroyed, being preserved only along the lingual edges of the cheek teeth. Suffice it to say that the posterior narial opening is just behind a line joining the posterior edges of the talons of the third molars. The pterygoids would seem to be moderately heavy, as would be necessary for the attachment of strong pterygoid muscles.

The basicranium is only partially preserved, but enough remains to give us a glimpse of certain of the anatomical features. As was pointed out above, the malars project widely at their posterior borders. This is an attribute of the wide glenoids, which indicate a mandibular attachment of considerable strength. In shape, the glenoids are like those of *Palaeochoerus*, with low borders along their sides, and with but slightly elevated postglenoid borders. The feeble development of the postglenoid border is a suid character, correlated with a rather free movement of the lower jaw during mastication. The bulla shows a precocious development towards the form typical of recent suids. It is very long and narrow (due to crushing the true width cannot be exactly determined) and it projects down to a distance almost equal to its

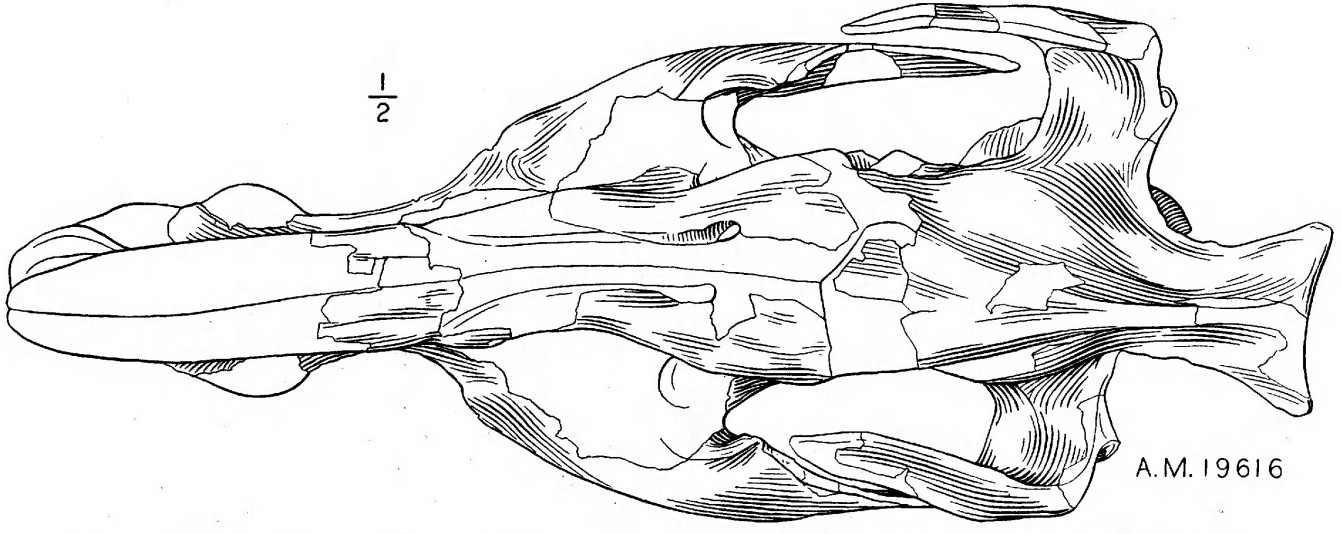

Fig. 2.—*Conohyus sindiense* (Lydekker). Amer. Mus. No. 19616. Top view of skull, one-half natural size.

length. This is a shape intermediate between the primitive bulla, which would be small and more or less globular, and that of the modern suids, in which the bulla is considerably deeper than it is long. The posterior half of the inner side of the bulla is joined to the basioccipital, and from this latter element a peculiar protuberance projects down on the inner side of the bulla. This connection between the bulla and the basioccipital causes the foramen lacerum medius to be quite separate from the foramen lacerum posterius. As in the modern suids, the foramen lacerum medius is confluent with the foramen ovale. The external auditory meatus is enclosed within a long tube, which runs along the back side of the glenoid, and its opening is directed backward and upward.

The paroccipital process is closely appressed to the posterior edge of the bulla, and naturally the stylomastoid foramen occupies a position intermediate between these structures. Only the proximal ends of the paroccipital processes are preserved, but it is presumed that they are relatively long, as is usual among the Suidae. Filhol has shown moderately long paroccipitals on *Palaeochoerus*, and naturally in connection with rather strong pterygoids, serving for the attachment of heavy internal pterygoid muscles, it would be expected that in the genus under discussion the paroccipitals would be well developed, in order to afford attachments for strong digastric muscles. Thus *Conohyus* shows its typically suilline affinities in the apparent strength of its masticatory muscles.

THE MANDIBLE.—The mandible, Amer. Mus. 19739, comes from the lower portion of the middle Siwalik beds, at a location four and one-half miles west of Hasnot, northern Punjab. Although coming from an horizon somewhat above that of the skull, the jaw is nevertheless of the same species, and so nearly identical are the lower molars, as compared to the corresponding teeth in the skull, that the two specimens, for the sake of comparative study, may be considered together. The mandible is relatively heavy, with a deep ramus, and with a broad ascending ramus and a fairly wide condyle. The symphysis is very strong and short, and it indicates a wide spread of the rami at the condyles. The anterior opening of the mental foramen is situated below the anterior border of the second premolar.

DENTITION.—The teeth of *Conohyus sindiense* have been described by Lydekker[1] and Pilgrim,[2] so it seems unnecessary to go into great detail on this subject. The specimens in the American Museum collection do, however, give a few additional points which were not seen in the original and more fragmentary material.

As has been demonstrated by Pilgrim, 1926, the genus *Conohyus* is distinguished by the enlargement of its second and third premolars,

[1]Lydekker, R. 1884. 'Siwalik and Narbada Bunodont Suina.' Pal. Indica. X, Vol. 3, Pt. 2, p. 95, plate 12, figs. 5–16.

[2]Pilgrim, G. E. 1926. 'The Fossil Suidae of India.' Mem. Geol. Surv. Ind., Pal. Indica. N.S., Vol. 8, No. 4, p. 12, Pl.ate 2, figs. 1–6.

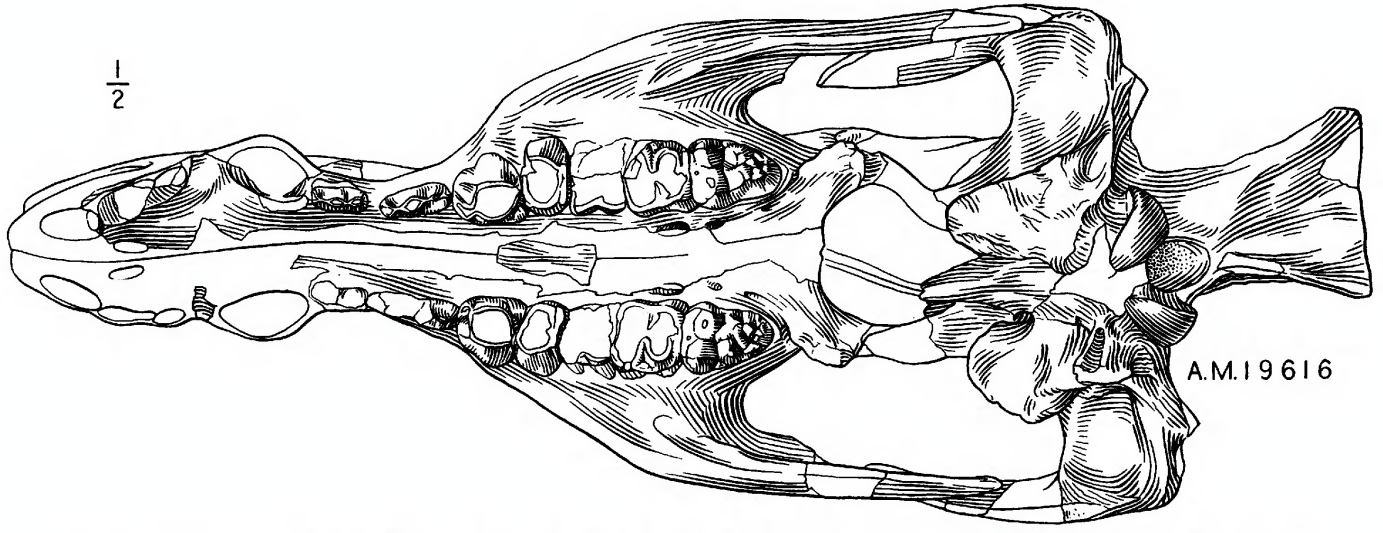

Fig. 3.—*Conohyus sindiense* (Lydekker). Amer. Mus. No. 19616. Palatal view of skull, one-half natural size.

this being a specialized character setting the Indian form apart from the typical European Miocene *Hyotherium*. The material at hand bears out the validity of Pilgrim's interpretation. In the upper dentition the teeth are all set closely together, there being but a slight diastema between the first and second premolars and another very short gap in front of the canine. The canine turns strongly outward. In both upper and lower jaws the incisors are crowded and immediately precede the canines, showing that there was no lengthening of the snout as in later pigs.

The first and second premolars above and below are very narrow teeth, each consisting of a central cusp, with a ridge running anteriorly and another posteriorly from it. The teeth posterior to the second premolars are as Pilgrim described them. His description may be summed up as follows. The third upper premolar consists of a large cone with a well developed but low cusp on the postero-internal corner of the tooth, and an anterior cusp. The fourth premolar is considerably wider than it is long, and when worn the outer and inner portions of the tooth become confluent. In the lower jaw the third and fourth premolars are single cones, the latter with an elevated posterior ridge. The first and second upper molars are four-cusped, with slight anterior and posterior cingula, while the third molar has in addition to the four cusps, a short talon, separated from the body of the tooth by a single median cusp. The first two lower molars are quadricuspid, and the last molar has, in addition to the talonid, two median conules.

TABLE OF MEASUREMENTS

SKULL	
Length, occ. cond. to tip of premaxilla (approximate)	277 mm.
Width, at glenoids	123
Preorbital length	164
Postorbital length (to condyles)	123
Ratio Preorbital : Postorbital :: 133 : 100	
Vertical diameter of orbit	37
Width across occ. condyles	40
Over all length (back of occiput-premaxilla)	317
MANDIBLE	
Length, condyle to anterior border of first premolar	182 mm.
Depth of ramus below first molar	45
Height of condyle above occlusal line	54

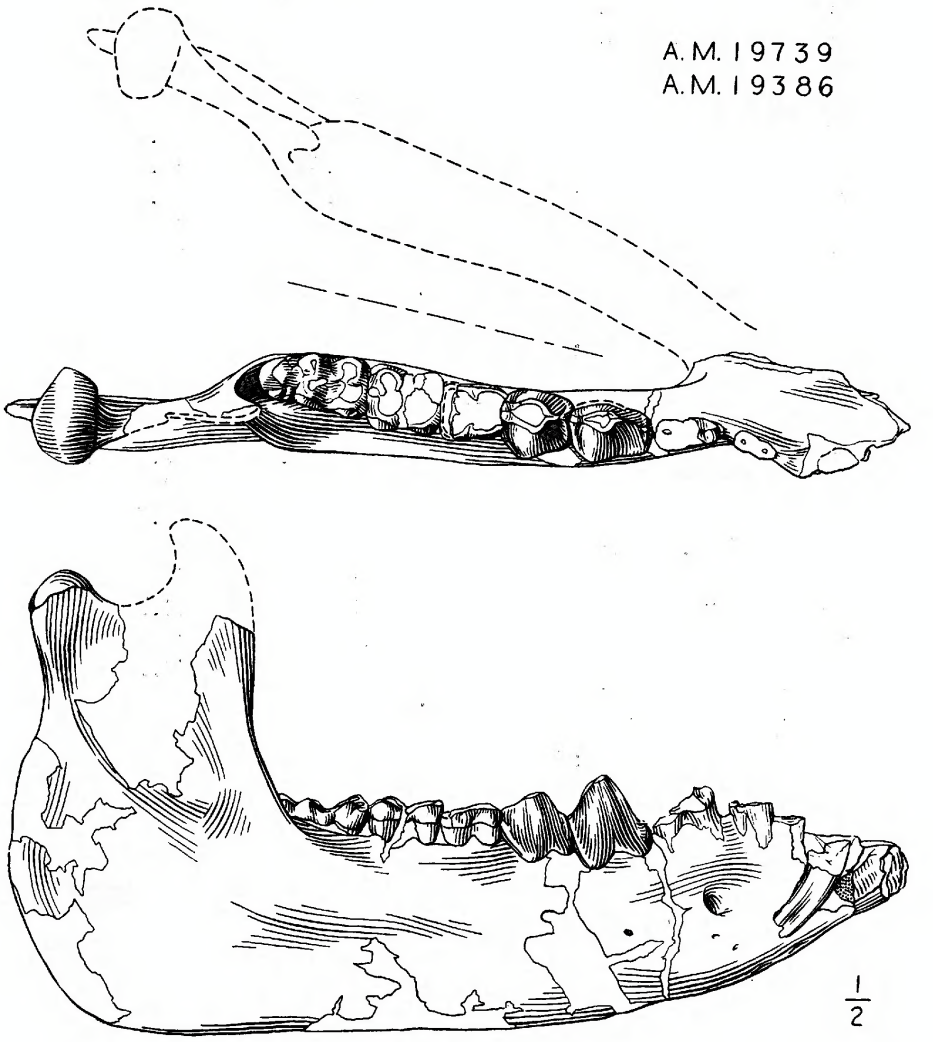

Fig. 4.—*Conohyus sindiense* (Lydekker). Amer. Mus. No. 19739. Mandible, with the third and fourth premolars and the first molar drawn in from Amer. Mus. No. 19386. Crown view above, and side view below. One-half natural size.

UPPER DENTITION, Amer. Mus. 19616

	Anteroposterior	Transverse
I^2 estimated from alveolus	10 mm.	5 mm.
I^3 " " "	7	4
C " " "	17	13
P^1	13	6
P^2	17	7
P^3	16	16.3
P^4	11.5	17.5
M^1	12.8	16.5
M^2	18	18
M^3	20	17

Premolar length	60 mm.
Molar length	52
Ratio	115 : 100

LOWER DENTITION, Amer. Mus. 19739

	Anteroposterior	Transverse
C	15 mm.	7.5 mm.
P_1	11	4
P_2	17	7.5
P_3 (From A.M. 19386)	18	14
P_4 "	16	15
M_1 "	14	11.7
M_2	18	15
M_3	26	14.7

Length of premolar series	65 mm.
Length of molar series	58
Ratio	112 : 100

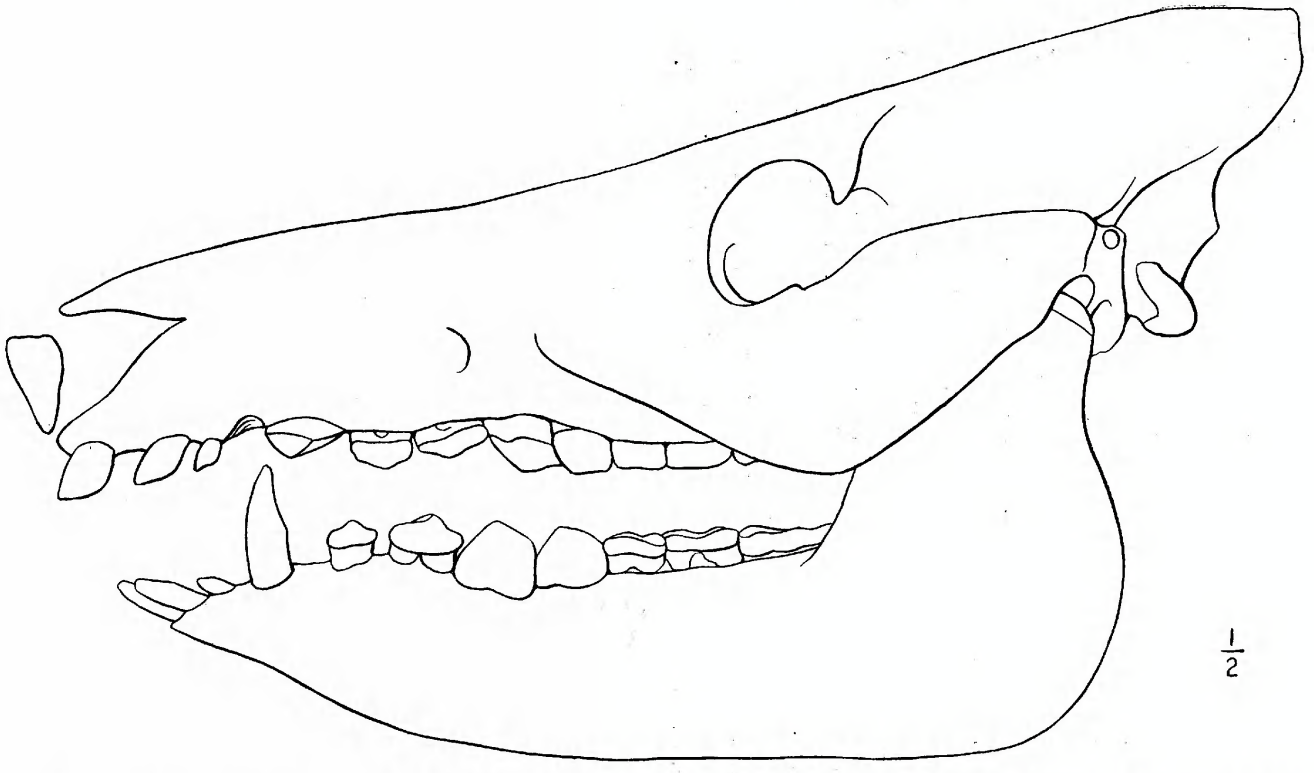

Fig. 5.—*Conohyus sindiense* (Lydekker). Restoration of skull and mandible, based on Amer. Mus. Nos. 19616, 19739, 19386, and figures by Filhol, Pearson and others. The shape of the os rostri is hypothetical. One-half natural size.

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